Reactive nitrogen requirements to feed the world in 2050 and potential to mitigate nitrogen pollution

Benjamin Leon Bodirsky\textsuperscript{1,2}, Alexander Popp\textsuperscript{1}, Hermann Lotze-Campen\textsuperscript{1}, Jan Philipp Dietrich\textsuperscript{1}, Susanne Rolinski\textsuperscript{1}, Isabelle Weindl\textsuperscript{1}, Christoph Schmitz\textsuperscript{1}, Christoph Müller\textsuperscript{1}, Markus Bonsch\textsuperscript{1}, Florian Humpenöder\textsuperscript{1}, Anne Biewald\textsuperscript{1} & Miodrag Stevanovic\textsuperscript{1}

Reactive nitrogen (Nr) is an indispensable nutrient for agricultural production and human alimentation. Simultaneously, agriculture is the largest contributor to Nr pollution, causing severe damages to human health and ecosystem services. The trade-off between food availability and Nr pollution can be attenuated by several key mitigation options, including Nr efficiency improvements in crop and animal production systems, food waste reduction in households and lower consumption of Nr-intensive animal products. However, their quantitative mitigation potential remains unclear, especially under the added pressure of population growth and changes in food consumption. Here we show by model simulations, that under baseline conditions, Nr pollution in 2050 can be expected to rise to 102–156\% of the 2010 value. Only under ambitious mitigation, does pollution possibly decrease to 36–76\% of the 2010 value. Air, water and atmospheric Nr pollution go far beyond critical environmental thresholds without mitigation actions. Even under ambitious mitigation, the risk remains that thresholds are exceeded.
Globally, approximately 425 Tg of reactive nitrogen (Nr) is fixed every year from unreactive atmospheric dinitrogen (N₂) by natural processes in the oceans, on land and by human activity. Nr is an important plant nutrient and about half of the globally fixed Nr fertilizes agricultural areas. Agriculture thereby became the major driver of the global nitrogen cycle, in which total (terrestrial and oceanic) fixation doubled and terrestrial fixation more than quadrupled since the industrial revolution. The nutrients reach the agricultural sector in the form of four major Nr sources: as inorganic fertilizers that were produced with the Haber–Bosch synthesis; as biologically fixed Nr, mainly driven by the cultivation of leguminous crops; through atmospheric deposition of Nr that previously volatilized elsewhere (about four-fifths stemming from anthropogenic sources); or through the release of organic Nr when soil organic matter depletes through soil management.

While passing through the agricultural supply chain, the Nr from these sources is subsequently lost on the field, in manure management, and as waste and sewage. As there is little long-term storage of Nr in the agricultural sector, Nr sources correspond approximately to Nr losses, and Nr are an easily communicable indicator for the disturbance of environmental systems by Nr pollution. The subsequent destinies of lost Nr are diverse. Denitrification converts most of the Nr back into unreactive N₂, but is also coupled to the production of the greenhouse gas and ozone-depleting substance N₂O. If nitrogen is lost in reactive form through leaching or volatilization, it can cause a cascade of effects on the environment. For instance, in combination with other nutrients, excessive Nr can lead to the disturbance of aquatic and terrestrial ecosystems through eutrophication. In the air, it leads to the formation of ozone and particulate matter. Negative impacts on human welfare include direct health damages like cancer and asthma, as well as the loss of ecosystem services, affecting for instance the productivity of aquatic ecosystems and hence fishing. In monetary terms, Nr pollution is estimated to cause damages in the magnitude of 0.3–3% of global gross domestic product (GDP).

To reduce agricultural Nr pollution, a number of key mitigation actions are available for fertilization, livestock management, societal consumption and waste recycling. However, it has not been quantitatively assessed by how much these mitigation measures could reduce Nr pollution at the global scale. Previous analysis of the global agricultural nitrogen cycle focussed mostly on the estimation of Nr flows in the present and past as well as reference scenarios for future Nr flows and nitrogen fixation. Quantitative estimates for Nr mitigation potentials are, so far, only based on simple calculations or do not provide a comprehensive overview over the available mitigation measures and their interactions.

We apply a land-use and nitrogen-budget model to analyse both reference and Nr mitigation scenarios for the global agricultural nitrogen cycle. Under different assumptions on consumption patterns and production technology, the model estimates the Nr sources required to satisfy a given future demand for agricultural products and assesses how the Nr is subsequently lost in the food supply chain. For a middle-of-the-road reference scenario, Nr sources can be expected to increase from currently 185 Tg Nr in 2010 to 232 Tg Nr in 2050. Nr pollution will thereby depart from environmental thresholds for air, water and atmospheric pollution. Subsequently, we analyse the following actions, which show substantial potential to mitigate Nr pollution: Reduced household food waste and recycling of food waste and sewage as fertilizers; lower share of animal-based calories in diets; efficient livestock management by improved feeding and higher recycling share for animal manure; and efficient fertilization of fields. The combined effect of all mitigation actions can lower Nr losses to 95 Tg Nr in 2050. The risk remains that this reduction is insufficient to bring Nr pollution below critical environmental thresholds. While leakage effects and externalities require a global approach to the regulation of Nr pollution, a spatial refinement of environmental thresholds is advisable for an efficient adaptation to Nr pollution.

**Results**

**Reference scenario.** Our reference scenario without Nr mitigation is parameterized according to the ’SSP2’ storyline of the shared socio-economic pathways. This middle-of-the-road scenario assumes a world population of nine billion people in 2050 and a global GDP that more than triples to 230 trillion US Dollars at 2005 prices and adjusted for purchasing power parity. Population groups which gain in prosperity demand a more affluent diet with a higher share of livestock products. Therefore, crop production for food and feed increases by more than 50% compared with 2010, mainly by intensifying existing cropland. Over time, the developing countries adopt the industrialized livestock management of the Western regions. Efficiency of Nr application on cropland improves in all world regions, but predominantly in the least efficient ones (Methods, Table 1).

According to this reference scenario, Nr sources rise from 185 Tg Nr in the year 2010 to 232 Tg Nr in 2050 (Fig. 1). This Nr stems mostly from inorganically fixed fertilizer (F) and biological fixation (B), and to a lesser extent from atmospheric deposition (D) and the release of Nr by the depletion of soil organic matter (SOM). Non-cropland-based Nr sources include fish and products from pasture-fed livestock (FF). While passing through the food supply chain, most of these nutrients are lost on the fields (LF), in household waste and sewage (LH, LS), and in animal waste management (LA). Other destinies (O) include post-harvest and processing losses, slaughter waste, the application of manure on pasture land and material use of agricultural products.

**Nr mitigation scenarios.** Subsequently, we estimate the effect of four Nr mitigation options on Nr sources and losses (Fig. 1). The options were parameterized according to what is thought to be their maximum feasible potential (see Methods for details). They comprise the key mitigation actions proposed by the assessment ‘Our Nutrient World’ for cropland production, the livestock sector, societal consumption and sewage. ‘Less household (HH) waste and recycling’ could lower Nr sources by 56 Tg Nr, removing the Nr losses that accrued in the production of wasted food, and recycling the nutrients from sewage and household waste to the fields. ‘Less consumption of animal products’ reduces Nr requirements by 30 Tg Nr, lowering losses in animal waste management as well as field losses by rendering parts of the feedstock production obsolete. ‘Efficient fertilization’ can reduce Nr losses on the field by 58 Tg Nr. ‘Efficient livestock management’ can lower required Nr sources by 27 Tg Nr through reduced losses in animal waste management and lower feedstock production.

The combination of all mitigation measures fundamentally alters the flows in the nitrogen cycle by 2050 (Fig. 2), and Nr losses are reduced to 95 Tg Nr. Crop biomass and grazed pasture are strongly reduced (C, P), and the dominant role of the livestock sector declines (A, P). Moreover, the absolute amount of recycled manure (RM) and crop residues (RR) as well as biological fixation (B) is reduced, but much less in relation to the savings of industrial fertilizer (F). The ‘full-chain efficiency’ expressing the share of newly fixed Nr arriving at the consumer is increased to 69%, considerably higher than the current level.
(22%) as well as the level projected in SSP2 for 2050 (29%), and it exceeds even the proposed long-term target of 50%1. In total, the required Nr sources are reduced by 138 Tg. The reduction potentials of the individual mitigation actions are not independent, such that the combined reduction potential is lower than the sum of the individual reduction potentials. For example, reduced household waste diminishes the demand for agricultural products, resulting in lower down-stream field losses and thereby reducing the mitigation potential of more efficient fertilization.

Sensitivity analysis. A sensitivity analysis, varying the major baseline and mitigation scenario parameters following the SSP 1 and 3 storylines shows that total Nr losses have an uncertainty range of at least 188–290 Tg Nr in the reference and 66–141 Tg Nr in the mitigation case.

Discussion
There are few additional mitigation options that are not covered by the analysed mitigation scenarios. These include lowering material use of agricultural products, abandoning the burning of crop residues or reducing and recycling processing waste (item O in Fig. 1). Our scenarios also did not consider morally problematic options like reducing population growth31, profound behavioural changes like diets solely based on leguminous proteins32 or technological breakthroughs occurring before 2050 such as cereals that fix nitrogen33. Finally, the cultivation of bioenergy crops to replace fossil fuels or to sequester CO2 was not considered in this study. Producing 100 Exajoule (one-fifth of current primary energy) of nutrient-efficient second generation bioenergy crops requires approximately 10 Tg of additional Nr sources, even under best practice conditions25.

Upper estimates of monetized damage caused by current agricultural Nr pollution are as high as the agricultural value added1,34. As mitigation costs are by orders of magnitude lower than damage costs35, ambitious mitigation action can be well justified. However, cost-benefit analysis should be used with care as this tool aggregates preferences based on the willingness (and therefore ability) to pay. Given the highly unequal global distribution of wealth, this may lead to ambiguous outcomes, as it may for instance value overconsumption and ambitious

**Table 1 | Scenario parameters, entering the Model of Agricultural Production and its Impact on the Environment (MAgPIE) for the middle-of-the-road reference and mitigation scenario of the shared socio-economic pathways (SSPs).**

<table>
<thead>
<tr>
<th>Year</th>
<th>1995</th>
<th>2010*</th>
<th>2050</th>
<th>2050</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scenario</td>
<td>Shared socio-economic pathway 2 reference</td>
<td>Shared socio-economic pathway 2 reference</td>
<td>Shared socio-economic pathway 2 mitigation</td>
<td></td>
</tr>
<tr>
<td>Population (bio)</td>
<td>5.7</td>
<td>6.8</td>
<td>9.1</td>
<td>9.1</td>
</tr>
<tr>
<td>GDP (trillion USD_05 PPP)</td>
<td>39</td>
<td>67</td>
<td>230</td>
<td>230</td>
</tr>
<tr>
<td>Per capita demand (kcal per capita per day)</td>
<td>2,677</td>
<td>2,841</td>
<td>3,178</td>
<td>2,731*</td>
</tr>
<tr>
<td>Household-waste (share of demand)</td>
<td>22%</td>
<td>25%</td>
<td>31%</td>
<td>19%</td>
</tr>
<tr>
<td>Animal-based calories in diet (share of demand)</td>
<td>16%</td>
<td>18%</td>
<td>22%</td>
<td>15%</td>
</tr>
<tr>
<td>Soil Nr uptake efficiency (SNUPE)</td>
<td>51%</td>
<td>53%</td>
<td>60%</td>
<td>75%</td>
</tr>
<tr>
<td>Feed efficiency† (J animal product per J feed)</td>
<td>3.3%</td>
<td>3.6%</td>
<td>4.3%</td>
<td>5.7%</td>
</tr>
<tr>
<td>Recycling quota of animal manure in confinement (share)</td>
<td>61%</td>
<td>64%</td>
<td>76%</td>
<td>90%</td>
</tr>
</tbody>
</table>

*Values for 2010 are already scenario parameters.
†Some countries do not reach the limit of 2,750 kcal per capita per day or the livestock share of 15% in the economic conditions of SSP2.
‡Average over all livestock products and regions weighted with the livestock production of 2010.

**Figure 1 | Sources and losses of reactive nitrogen in the agricultural food supply chain in 2050.** Units are in Teragram (Tg) reactive nitrogen (Nr). All scenarios are based on the storyline of the middle-of-the-road scenario of the shared socio-economic pathways (SSP2), while they differ in respect to the implemented mitigation measures.
environmental standards in rich countries higher than food security and a healthy environment in poor countries.

To keep the Earth system within favourable conditions for human welfare, it was proposed to limit anthropogenic Nr fixation from all sectors below a ‘planetary boundary’ of $35\text{Tg}\text{Nr}$, a value that would be far exceeded even with our mitigation scenarios. However, the height of this first and deliberately preliminary target was criticized to be arbitrary and unnecessarily low to avoid most pollution damage and also too low to provide food security.$^{10,36,37}$ A recent study$^{10}$ developed updated thresholds for air, water and atmospheric Nr pollution based on critical Nr concentrations (see Methods). Comparing Nr losses of agriculture with these critical thresholds (Fig. 3) reveals that current pollution already exceeds all of these thresholds. Moreover, our results indicate in accordance with most other baseline scenarios$^{4,19–21,38}$ that Nr pollution will probably continue to rise and further depart from these thresholds$^{10}$.

We show with this analysis that even under ambitious mitigation action, it remains uncertain whether water and atmospheric pollution can be reduced below the global critical thresholds in 2050, despite the substantial mitigation potential in crop farming, animal husbandry, food consumption and waste management. Due to the uncertainty of pollution projections and of appropriate thresholds, constellations are possible in which all respective thresholds are exceeded. Not represented in these ranges is the additional considerable uncertainty, which is connected to estimates of most Nr flows even for the current state$^{39}$, in particular in regard to emissions$^{4,5}$. Impacts of pollution are not linearly connected to the quantity of Nr losses, but are also determined by the distribution of Nr losses and vulnerable receptors in time, space and chemical form. Adapting to Nr pollution that cannot be mitigated is therefore the subsequent step to avoid damages, and possibly allows the loosening of environmental thresholds in places or times of low vulnerability. The above critical thresholds are therefore only a first step towards such a damage-minimizing distribution, and should be refined to a spatial and temporal explicit level.

Still, the problem of Nr pollution has to be tackled with a global perspective. This is obvious for the greenhouse gas and ozone-depleting substance N$_2$O, which disperses evenly in the atmosphere. This is obvious for the greenhouse gas and ozone-depleting substance N$_2$O, which disperses evenly in the atmosphere.
atmosphere independent of the point of loss. But also for short-range pollutants, ambitious local environmental thresholds may lead to a shift of pollution sources to regions that fail to enforce environmental standards. Similarly, the required mitigation actions, like reducing food waste, do not only reduce local but also global environmental impacts. As these positive externalities cannot be fully internalized under uncoordinated local policies, global cooperation would be conducive when regulating Nr pollution.

Methods

Land-use model. The projections were made using the Model of Agricultural Production and its Impact on the Environment (MAgPIE)4,24-27,29-36. Revision 7294. MAgPIE is a mathematical programming model that is used to create long-term scenarios and assessments of global land use. For a given food demand, the model estimates cost-optimal production patterns, and simulates major dynamics of the agricultural sector, like trade, technological progress and land allocation according to the scarcity of suitable land, water and economic resources4. As it treats agricultural products not only as economic values but also as physical goods, MAgPIE can perform analysis of material flows. The products in the model comprise 17 crop groups, each with individual above- and belowground crop residues, five livestock production types, eight types of conversion by-products originating from food processing, grazed pasture and scavenging. Products can be used for food, feed, other use (comprising material use and waste in the production chain) and seed, wherever applicable. Crop residues can be recycled to soils, burned in the fields, used as feed or used as material4. The demand for food enters the model as an exogenous trajectory28,30. Demand for material consumption and production waste is assumed to grow over time in proportion to food demand, while the demand for feed is a fixed share of crop production4.

The demand for feed depends on the quantity of livestock production, as well as regional and livestock-specific feed baskets. In a first step, feed energy requirements per livestock product are calculated that entail the minimum requirements for maintaining growth, lactation, reproduction and other basic biological functions of the animals. In addition, they comprise a general allowance for basic activity, temperature effects and expenditures for grazing. In a second step, these feed energy requirements are settled with regional livestock-specific feed baskets comprising concentrate feed, conversion by-products, crop residues and grazed biomass. The data available on the amount of grade I and II crop residues was assumed to provide the remainder to fulfill the energy requirements of animals. The feed was distributed between the animal groups based on digestibility rules. Future developments within the livestock sector are implemented via convergence of the feeding systems to feed baskets that are parameterized according to the storyline, that is, a convergence to intensive European systems with high feed efficiencies and a higher share of concentrates27.

The production of crops requires financial resources as well as land and water41. Cropland expansion leads to additional costs and is limited by biophysical conditions as well as by competing land-use activities. In addition to land expansion, the model also invests into yield increasing research and technology42. Crop growth functions connect crop harvest to the production of above- and belowground residues4. Similarly, the production of conversion by-products depends on fixed conversion factors multiplied with the regional crop supply35. Finally, livestock production requires financial resources, feed and water. To match regional and national data, MAgPIE optimizes global land-use patterns and trade flows to minimize financial costs24. To account for trade restrictions and distortions, the socio-economic world regions have to produce a certain share of their internal demand25. The optimization problem is solved in consecutive time steps from 1995 to 2050, whereby the cropland area and the level of technology are passed on from one time step as input data to the consecutive time step4.

Nr budget module. MAgPIE was extended by a Nr flow module4 that transforms all biomass flows in the model into Nr flows. The closed budget approach and a consistent connection of all Nr flows guarantee that the sum of Nr fixation, Nr release and inflows from other sectors corresponds to the sum of Nr losses and Nr flows to other sectors. Similarly, intermediary closed budgets are also used on a regional level for cropland soils, distribution and processing of agricultural products, livestock feeding, manure management and the household sector. While certain processes in MAgPIE such as crop production and water use are simulated spatially explicit on the level of clustered 0.5° grid cells, Nr flows and Nr budgets are calculated on the level of 10 world regions5.

Nr in harvested aboveground (RR) and belowground (RB) crop residues are estimated based on crop-specific growth functions and Nr contents of the individual plant components. The Nr derived from biological fixation within plants (B) is estimated based on plant-specific share of plant Nr derived from atmospheric fixation, while biological fixation by free-living microorganisms and denitrification are estimated based on Nr fixation per cultivated area. All belowground crop residues are assumed to be recycled to the field (RBB). In contrast, aboveground crop residues have to settle first the demand for feed from the livestock sector; moreover a fixed share of crop residues is assumed to be used for material purposes or is lost when residues are burned on the field. Only the remaining residues are recycled on fields (RRA). The Nr, which is released on croplands when soil organic matter depletes after the opening of new cropland (SOM), is calculated on the basis of model-endogenous land-use change activity, spatial-explicit carbon contents of natural soils, typical climate-specific temperature effects and expenditures for grazing. In a second step, these requirements are distributed among different agricultural systems according to regional shares that change over time with scenario assumptions. Depending on their management, different shares of the nutrients are lost to volatilization and denitrification (LA); the remainder is recycled as organic fertilizers on cropland (RM) and pasture (RP)45.

For this study, the model was extended for a more detailed representation of food intake, food waste and sewage. Total food demand (intake + waste) and the share of animal-based products are estimated based on regression models46-50. The contribution of aquatic products to the protein supply by animal-based products is held constant at the value of year 2005 (ref. 43). To estimate household food waste, we assumed that the minimum share of households in all countries is 15%, accounting for inevitable losses and non-edible items like bones, kitchen, husks and peels4. Moreover, we assumed based on plausible regional intake estimates for developed regions45 that the per capita demand exceeding 2,200 kcal per capita per day is provided as non-Nr waste. The resulting regional waste share is assumed to be lower than estimates44, but are dynamic for the future when per capita food demand rises. TheNr in sewage was estimated as the non-wasted share of food supply, not accounting for the relatively small share of Nr that is accumulated in human bodies or lost in sweat, hairs and nails5. Depending on the scenario assumptions, a share of sewage and organic waste is recycled to fields (RS, RW) or lost into the environment (LS, LW).

Central to the model are regional nutrient budgets for cropland soils, which are used to determine the future requirements of fertilizers. Different Nr inputs to croplands have different fertilizer equivalents4, as they are to a different degree subject to losses on the field. Homogeneous Nr inputs (for example, industrial feed) are assumed that can be easily distributed over the field have high equivalence values, while inhomogeneous Nr inputs (for example atmospheric deposition) have low equivalence values as their quantity, spatial distribution and timing cannot be controlled. Using a simplified approach, we distinguish only two categories in MAgPIE: First, Nr inputs from seed (S) and biological fixation within the plant (B) are not taken up from the soil, and hence are not subject to losses by volatilization, leaching or denitrification. Nr from these inputs is therefore assumed to be fully incorporated into plant tissue. Second, we assume that all other Nr inputs are subject to losses before plant uptake and that only a share of the applied Nr inputs are withdrawn by the plant roots and incorporated into plant biomass. This share, named as soil Nr uptake efficiency (SNUPE), is a regional model parameter which reflects next to the climatic and biophysical conditions mostly the fertilization technology of farmers. As we do not consider the differences in fertilizer equivalences between individual soil Nr inputs like manure and inorganic fertilizers, a high value for SNUPE also implies that inhomogeneous Nr inputs can be better integrated into crop fertilization, for example, by improved monitoring or by manure processing4.

To calculate the application of inorganic fertilizers (F), we estimate the fertilization requirements to obtain a certain production under a given fertilization technology level. The Nr withdrawals from crop production (H + RA + RB) and theNr in soil (SNUPE) determine the required Nr inputs from organic or inorganic fertilizers (equation (1)). Based on the availability of organic fertilizers, it is ultimately determined which amount of inorganic fertilizers is needed to balance out the budget.

$$H + RA + RB = SNUPE \cdot (F + RM + RRA + RBB + D + B2 + SOM + RH + RS) + 1^1 (S + B1) \; \; \; \; (1)$$

The difference between inputs and withdrawals represents the field losses (LF) by denitrification, leaching and volatilization (equation (2)).

$$LF = F + RM + RRA + RBB + D + B2 + SOM + RH + RS + 5 + S + B1 - H - RA - RB \; \; \; \; (2)$$

A comprehensive overview over the estimates for the respective Nr flows can be found in the Supplementary Data 1.

Environmental thresholds. The environmental thresholds for Nr pollution were adopted from a study51 that estimates ‘planetary boundaries’ for Nr-related air,
water and atmospheric pollution. For air pollution, a critical threshold was determined by limiting spatially explicit ammonia concentration to current levels; moreover concentration levels were capped where they exceed a maximum concentration (1–3 g m⁻³). Likewise, water pollution was estimated based on maximum concentrations of Nr in surface water (1–2.5 mg Nr l⁻¹). Critical thresholds for atmospheric pollution were estimated based on nitrous oxide (N₂O) emission trajectories leading to global warming targets (1–2.6 W m⁻²).

For total agricultural Nr losses, the study²⁸ provides a risk indicator RNRcritical = N compounds critical / NR present in the year 2000 has to be reduced in order to reach the critical thresholds for Nr pollution. Assuming that the ratio between N fixation and Nr losses does not change, they multiply RNRcritical by the agricultural nitrogen fixation of 121.5 Tg Nr in the year 2000 to derive thresholds for nitrogen fixation. However, total agricultural Nr losses is a more meaningful indicator for Nr pollution than total agricultural Nr fixation, as Nr losses also include Nr from sources like atmospheric deposition that may evolve disproportionately in the future. Therefore, to derive the thresholds for Nr losses we multiplied our estimate of Nr losses present in Fig. 3, we multiplied their risk indicator RNRcritical with our estimate for total Nr losses in the year 2000 (159 Tg Nr) instead of multiplying with total nitrogen fixation.

The above critical thresholds are derived on the assumption that critical concentrations are not exceeded at any point of space. This assumption is not represented within MAGIC, which calculates Nr flows only on the level of world regions. Especially on highly productive sites, thresholds are likely to be exceeded in our scenarios. Limiting production on these sites would lead to increased land expansion elsewhere with negative consequences on other environmental systems.

**Description of mitigation scenarios.** The scenario ‘Less household (HH) waste and recycling’ assumes a reduction of the waste share to 20%, resulting in a cut of per capita demand of each country to 2,750 kcal (2,200/0.8) in the year 2050. This is lower than the daily global per capita average in 2005 of 2,787 kcal, and considerably lower than the OECD average of 3,444 kcal³. Furthermore, we assume that half of the nutrients in household waste and sewage are recycled as fertilizers. The scenario ‘Less animal products’ assumes that no country derives more than 15% of its calories (29% of proteins) from animal-based products. This corresponds to a ‘demitarian’ western diet⁴, in which the share of animal-based calories is half of the current level in Western regions, and reverts the trend of the reference scenario to a ‘demitarian’ western diet⁴, in which the share of animal-based calories is half of the current level in Western regions, and reverts the trend of the reference scenario (Table 1).

The scenario ‘Efficient fertilization’ estimates the effects of increasing SNUPE. High SNUPEs are difficult to reach, as this requires fertilizing the right amount of the right fertilizer at the right time and right place (4R), but also a better spatial and temporal pattern of fertilizer application and manure management. The spatial patterns of global fertilizer application and manure production. Earth Interact. 14, 1–22 (2010).


IIASA, SSP Database (2013).


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Author contributions
B.L.B., A.P. designed the study and analysed data. B.L.B. wrote the paper, with important contributions from A.P., C.M., H.L.-C., S.R. B.L.B., H.L.-C., J.P.D., C.S., I.W., A.P., M.B., F.H., M.S., S.R., A.B. developed and improved the model. All authors discussed the results and commented on the manuscript.

Additional information
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